On the Development of the Auditory Apparatus in Sphenodon punctatus.

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(Abstract.)

This memoir contains a detailed and fully illustrated account of the development of the auditory apparatus and associated structures in the New Zealand Tuatara. As this important type is on the verge of extinction, it was thought desirable to treat the subject fully, although, as might have been expected, the developmental history agrees closely with that found in other reptiles.

The work was carried out chiefly by means of wax plate reconstruction models. The development of the pharynx and its derivatives, the thyroid and thymus glands and the trachea, was investigated and appears to follow the normal course. The first visceral cleft undergoes some closure from below upwards and the process is completed by the apposition of the anterior and posterior borders of the cleft. The second and third visceral clefts are closed by a backwardly-growing operculum, while the fourth visceral pouch is imperforate and bears a rudimentary fifth visceral pouch as an evagination of its posterior surface.

The apparent absence of separate dorsal and ventral divisions of the visceral clefts whereby all or any of the first three pairs of visceral pouches communicate with the exterior would seem to be an indication of the primitive nature of this reptile. With this possible exception, the present observations do not reveal any abnormalities in the developmental changes undergone by the pharynx or by such of its derivatives as have now been considered.

The existence of two pairs of head cavities was confirmed, those of each pair communicating with one another by transverse canals. The head cavities appear to originate by the splitting of a single pair of cavities, and, at a later stage of development, there appear—in the regions formerly occupied by them—rounded mesoblastic masses which may be "premuscle masses." It is suggested, therefore, that each head cavity should be regarded as a "myocœle," but that the head cavities represent the cavities of the head somites is uncertain, as is also their suggested connection with the orbital muscles.

The vascular system was found to exhibit a number of primitive features. The arteria basilaris originates as a pair of completely separated vessels, and

the progressive fusion subsequently undergone by these primitive arteries supports the suggestion advanced by Dendy (1909) that the (incompletely-fused) condition of the arteria basilaris observed by him in adult Sphenodon is reminiscent of an earlier paired condition, and is therefore a primitive feature. The development of the persistent ductus arteriosus and ductus caroticus, the relationship of the arteriæ laryngealis, pulmonalis and cervici muscularis, and the progressive reduction and ultimate fate of the aortic arches have all been investigated. It has also been shown that Sphenodon is similar to other reptiles in respect of the persistence and primitive nature of the arteria stapedialis, which is derived from a persistent dorsal vestige of the second aortic arch. The presence of a number of newly-identified branches of this artery (the arteriæ tympanica, dentalis inferior, temporalis posterior and auricularis posterior) has also been recorded. As regards the venous trunks of the auditory region the most conspicuously primitive features are the persistence of the tenæ cephalicæ, mediæ and posteriores and their relationship to the vena capites lateralis and to the primitive head-veins of the early embryo. The presence and development of paired venæ faciales, tympanicæ, and cochleares have now been recorded for the first time.

It is concluded that the arrangement of the blood vessels in the auditory region of Sphenodon is similar to, but more primitive than, that found in Lacertilia.

The region investigated includes cranial nerves vi—xii, the development of which was worked out in detail. The primitive facial nerve early shows differentiation into one pre-trematic and one post-trematic branch. The former gives rise to the ramus palatinus, while from the latter develop the ramus communicans interna, the chorda tympani and the ramus hyomandibularis. From the last-named trunk spring the delicate ramus recurrens and also the ramus communicans externa which passes ventral to the stapes and, ultimately uniting with the ramus communicans interna, enters the ganglion petrosum.

The development of nerves vi, ix, x and xi presents no abnormal features. Within the foramen jugulare the roots of nerves ix, x and xi enter an incompletely-trilobed ganglion of which the three component bundles of fibres are clearly differentiated and between which the passage of few communicating fibres can be observed. The roots of nerve xii undergo, as development proceeds, a progressive reduction in number from five to two, the foramina by which they emerge from the exoccipital region of the parachordal plate being similarly reduced in number from four to two.

The general development of the inner ear and auditory nerve is thoroughly normal. The auditory organ appears as a nearly circular, and slightly hollowed

patch of single-layered epiblast which rapidly develops into a deep auditory pit. Rapid upward growth of the ventro-lateral border of the pit ensues, the auditory pit being converted into an auditory sac (otocyst), the lumen of which communicates with the exterior by a narrow primitive ductus endolymphaticus.

The distal portion of the acustico-facialis neurencytium, by which the sensory end-organ was connected with the hind-brain, undergoes a simultaneous progressive differentiation into a dorsal or auditory and ventral or facial ganglionic rudiment, still united proximally to the hind-brain by a common root. The superficial area of the otocyst undergoes rapid expansion and it soon becomes constricted into a pars superior and a smaller pars inferior. The constriction passes through the large patch of neuroepithelium (primitive auditory epithelium)—which now occupies nearly the whole of the medial and a portion of the ventral wall of the otocyst—and divides it into two parts, each of which is connected with a portion of the auditory neurencytium.

The subsequent further division of these primitive sensory epithelial patches into the various maculæ acusticæ is accompanied by a corresponding division of the distal portion of the auditory neurencytium, which thus ultimately gives rise to the various ramuli of the auditory nerve. The present investigation confirms the suggestion that "the breaking up of the primitive auditory ganglion is a necessary accompaniment of the process of resolution of the sense-epithelium patch into its various macular areas" (Cameron and Milligan, 1910). The final closure of the otocyst takes place just dorsal to the middle of the lateral surface of the developing ductus endolymphaticus, and a protrusion of the medial surface of the same region now occurs, thus producing the rudiment of the saccus endolymphaticus. It is noteworthy that a vestige of the distal portion of the ductus endolymphaticus, now separated from the superficial epiblast of the head, persists in the oldest Sphenodon embryos examined, in which it occurs as a conical prolongation of the dorsal region of the saccus endolymphaticus situated in a foramen sacci endolymphatici piercing the cranial roof of either side, not far from the mid-dorsal line. This is obviously a primitive feature and has not been recorded in any of the higher Vertebrata.

The aperture by which the lumen of the ductus endolymphaticus communicates with that of the otocyst now undergoes displacement in a medio-ventral direction, owing chiefly to the expansion of the surface of the latter in a dorsolateral direction, although the process appears to be due, in part, to a ventral elongation of the closed portion of the ductus, which results from a progressive lateral fusion of its anterior and posterior walls, thus shutting off more and more of its lumen from that of the otocyst.

Simultaneously with this process there occurs a differentiation of the pars superior into a system of communicating canals and sinuses. These are formed by the outgrowth of a number of pockets and the ingrowth of the walls of a number of deepening grooves. The septa formed by these double-walled epiblastic folds and by the mesoblast included between them result in the formation of a central tri-radiate utriculus, the extremities of which are united by an anterior vertical, a posterior vertical, and a horizontal semicircular canal, each of which possesses a dilated "ampulla," on the floor of which arises a sensory crest or crista acustica. To each of these is distributed a ramus of the auditory nerve. On the medial wall of the utriculus occur a number of sensory epithelial patches, derived, like the epithelium of the cristæ acusticæ, from the neuroepithelium of the pars superior. These macular areas are at first united with one another and with the neuroepithelium of the pars inferior by tracts of neuroepithelium, but in the adult organ they are entirely separated.

The appearance of the grooves and pockets of the pars superior suggests that the anterior vertical and horizontal semicircular canals are formed somewhat earlier than the posterior vertical canal, but, on the other hand, the crista acustica of the horizontal semicircular canal appears to develop somewhat later than do those of the other canals. The development of the canals, the macular areas, and the branches of the auditory nerve has been fully investigated. A well-developed macula neglecta and a nerve ramulus supplied to it were found and the presence of a similar nerve-branch passing to the ductus endolymphaticus was noted. No sensory epithelium was, however, discovered in the saccus endolymphaticus. The pars inferior meanwhile undergoes differentiation into sacculus and cochlea, the latter exhibiting a curved distal pars lagenæ and a proximal pars basilaris, each with its own macular area and nerve supply.

A complete account of the histology of the inner ear was not attempted, but sufficient data have been obtained to confirm and supplement the histological details recorded by Osawa (1898). The maculæ and cristæ acusticæ contain hair-cells (auditory sense epithelium cells) and interstitial (supporting) cells, while the non-sensory areas of the inner ear consist of flattened or cubical epithelium, supported by an external investment of spindle connective tissue.

A detailed investigation of the development of the auditory capsule, columella auris, and associated bones was undertaken, special care being taken to examine a number of embryos in which chondrification of the rudiments of these structures had not yet occurred. The conditions obtaining in such early embryos have now been recorded for—it is

believed—the first time, and a full account of the developmental changes undergone by the cartilaginous structures of the auditory region has been given. That the cartilaginous auditory capsule and the anterior cornu of the hyoid are products of two connective-tissue proliferations, and that two centres of chondrification—one hyoidean and one capsular—originally separated by an intervening tract of mesenchyme, are found is indisputable, and, as a result of an examination of the developmental changes undergone by these structures, further information respecting the much-debated question as to the origin and relationships of the columellar apparatus has been obtained.

It is concluded that the columella auris is derived from the hyoid arch, with which it is continuous throughout all stages of development, and that the extra stapedial cartilage is primarily united with the anterior cornu of the hyoid. The supra-stapedial cartilage (including the recurrent process) is developed, and persists as an outgrowth from the extra-stapedial cartilage, and is therefore a hyoidean derivative.

The auditory capsule contributes, at most, a portion of the foot-plate of the stapes, which is probably partly capsular and partly hyoidean in origin. The distal portion of the stapes is exclusively hyoidean. At no period of its life history does Sphenodon possess any cartilaginous attachment between the supra-stapedial cartilage and the cranium, but, during the later stages of the embryonic period, and in adult life, there is a secondary attachment between, and partial fusion of, the supra-stapedial process and the quadrate.

The development of the tympanic cavity, functional tympanic membrane, extra-columellar sinew, and chorda tympani is described. It is noteworthy that, as in the thick embryo, the dorsal portion of the anterior tympanic diverticulum undergoes isolation, and finally disappears.

The results now obtained support the contention advanced by Gray (1913) that, while the inner ear of Sphenodon differs but little from that of other Reptilia—with the exception of Crocodilia—the middle ear really represents a transition stage in the evolution of the middle ear of the living Reptilia.